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Variation in litter decomposition-temperature relationships between coniferous and broadleaf forests in Huangshan Mountain, China

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Abstract: A study was conducted to identify the differences in the decompositions of leaf litter, lignin and carbohydrate between coniferous forest and broadleaf forest at 20°C and 30°C in Huangshan Mountain, Anhui Province, China. Results showed that at 20°C mass loss of leaf litter driven by microbial decomposers was higher in broadleaf forest than that in coniferous forest, whereas the difference in mass loss of leaf litter was not significant at 30°C. The temperature increase did not affect the mass loss of leaf litter for coniferous forest treatment, but significantly reduced the decomposition rate for broadleaf forest treatment. The functional decomposers of microorganism in broadleaf forest produced a higher lignin decomposition rate at 20°C, compared to that in coniferous forest, but the difference in lignin decomposition was not found between two forest types at 30°C. Improved temperature increased the lignin decomposition for both broadleaf and coniferous forest. Additionally, the functional group of microorganism from broadleaf forest showed marginally higher carbohydrate loss than that from coniferous forest at both temperatures. Temperature increase reduced the carbohydrate decomposition for broadleaf forest, while only a little reduce was found for coniferous forest. Remarkable differences occurred in responses between most enzymes **(**Phenoloxidase, peroxidase, β-glucosidase and endocellulase**)** and decomposition rate of leaf litter to forest type and temperature, although there exist strong relationships between measured enzyme activities and decomposition rate in most cases. The reason is that more than one enzyme contribute to the mass loss of leaf litter and organic chemical components. In conclusion, at a community scale the coniferous and broadleaf forests differed in their temperature-decomposition relationships.

Keywords: *Castanopsis eyrei*; Mass loss; Lignin; Carbohydrate; Temperature; Decomposition; Enzyme; Leaf litter

Introduction

Plant litter decomposition plays a critical role in the processes of nutrient cycling and organic matter turnover within ecosystem, and these processes are important determinants for plant productivity and ecosystem carbon storage (Petersen and Luxton 1982; Vitousek 1982; Aerts 1997). Carbon (C) stores in ecosystem represents a balance between net primary productivity (NPP) and C loss via organic matter decomposition (Freeman *et al*. 2001; Schilesinger and Lichter 2001; Cleveland *et al*. 2006).

Coniferous and broadleaf forests are typical succession stage of subtropical evergreen broadleaf forest. Coniferous forest is the early stage in the succession trajectories and broadleaf forest is the climax of forest ecosystem. These forests play an important role in global carbon dynamics, due in part to their high rates of growth and nutrient turnover compared to mature forests (Brown and Lugo 1990; Hughes *et al*. 1999). However, the floristic composition and forest structure may have changes during secondary succession (Brown and Lugo 1990), and the major changes are usually accompanied by marked shifts in the composition of the soil microbial community (Parmelee 1995). The structure of the soil microbial community involves in the decomposition of organic matter in forest ecosystems and is influenced by the amount and quality of litter input dependent on the plant species composition (Bååth *et al*. 1995; Pennanen 1999; Reith 2002). Vegetation cover directly and indirectly influences environmental variables and often has a dominant effect on the spatial patterning of soil microbial communities. This is particularly evident for trees modifying the environment and underlying soil properties. The application of geo-statistical techniques has also shown that the spatial distribution of microbial communities in forest soils is related to the location of different tree species and the associated ground flora (Pennanen *et al*. 1999; Saetre 1999). Soil microorganisms are the driving force for the decomposition process in forest (Salamanca 2002). The changes in structure and composition of the decomposer community will inevitably affect the balance between the gain and loss of C during decomposition (Schulze *et al.* 2000). We need to understand whether carbon balance differs among forests.

Besides the decomposer microorganism community, climate is another main factor controlling litter decomposition (Bargali *et al*. 1993; Austin and Vitousek 2000; Tian *et al*. 2000; Guo and

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Sims 2001). Climate warming has remarkable effect on balance of C storage. It is suggested that decomposition rate is faster than that rate of NPP with increasing temperature. Consequently, soil C storage may decrease as the response to climate warming (Hyvönen *et al*. 2002). Temperature response of decomposition is determined largely by the type of functional groups of microorganisms, thus temperature-decomposition relationship probably varies among forests.

The objective of this study is to determine the relationship between temperature and decomposition in coniferous and broadleaf forests in Huangshan Mountain. Further, we focus on explaining the difference in temperature control of decomposition between coniferous and broadleaf forests at a community scale. Our general working hypothesis is that at a community scale the coniferous and broadleaf forests differ in their temperature-decomposition relationships.

Materials and methods

Field sites and sampling

Coniferous forest stand and broadleaf forest stand, dominated by *Pinus massoniana* and *Castanopsis eyrei*, respectively, were selected in Huangshan Mountain, Anhui Province, China. The two stands are located at elevations of approximately 600 m. The average annual temperature is about 15.5°C. During the summer days, the average temperature is about 20°C and the highest temperature reaches 37.5°C. The annual rainfall is 1 540 mm. The soils at two sites are classified as yellow soil. A more detailed description on the research locations is given by Zhang *et al*. (1997).

A sampling plot of 20 m×20 m in size was chosen in each forest stand and subdivided into 16 subplots (5 m×5 m). In each subplot, a 10 cm × 10 cm quadrat was selected at random. The organic layer in 5-cm depth of each quadrat was sampled with polypropylene bag. The samples were transported back with ice bags and stored at 4°C in the Lab. of Plant Science, Nanjing University. At the same time, freshly abscised leaves of *Castanopsis eyrei* were collected for the laboratory decomposition experiments. All samples were obtained in October, 2005.

Laboratory design

The experiment was designed to analyze the effects of temperature and forest type on the decomposition. A 20°C treatment modeled the current annual mean temperature and a 30°C treatment modeled the high temperature in summer days of subtropical evergreen forest in Huangshan Mountain.

The organic layer samples from each stand were chopped (about 2 mm × 2 mm squares) and then thoroughly mixed to obtain suspension of microorganism decomposer. A 25-g oven-dry equivalent of field-moist organic layer sample was homogenized with 500 mL de-ionized water in a blender for 30 s. The solution was then filtered through a 1-mm nylon mesh to obtain resultant suspension of microorganism decomposer (Sjöberg *et al*. 2004; Ayres *et al*. 2006).

To prepare leaf litter sample, leaf disks were punched out with a cork borer (1 cm diameter). A sub-sample for obtaining weight loss was included in each treatment. Another sub-sample was prepared for enzyme analyses. Leaf disks were pressed by moistened paper towels between the base and lid of a Petri dish (9 cm in diameter), then autoclaved at 120°C for 20 min.

The sterilized disks were placed on surfaces of Petri dishes containing 20 mL 2% plain agar. The disks were then inoculated with 5-mL test suspension of microorganism decomposer and incubated at temperature of 20°C and 30°C, and relative humidity of 90% in darkness for 5, 30, 60, 90, 120 days. To ensure a homogenous inoculation of the microorganism decomposer, the 5 ml aliquots were removed from the suspension under constant stirring.

Organic component analyses

A sub-sample of leaf litter was oven-dried at 75°C for 48 h to constant weight for determining the mass loss and other analysis. The dried litter samples were ground in a laboratory mill (0.5 mm screen). Lignin concentration of the samples was estimated by gravimetry using hot sulfuric acid digestion (King and Health 1967; Osono and Takeda 2002). A 50-mg sample was extracted with alcohol-benzene and the residue treated with 72% sulfuric acid (v/v) for 2 h at room temperature with occasional stirring. The mixture was then diluted with distilled water to make a 2.5% sulfuric acid solution and autoclaved at 120°C for 1 h. After cooling, the residue was filtered and washed with water through a porous crucible (G4), dried at 105°C and weighed as acid-insoluble residue. The total carbohydrate analysis used by filtrate (autoclaved sulfuric acid solution) was described as below.

Total carbohydrate in the filtrate was estimated by the phenol-sulfuric acid method (Osono and Takeda 2002). The filtrate was added with 5% phenol (v/v) and 98% sulfuric acid (v/v). The optical density of the solution was then measured by a U-30000 spectrophotometer (Hitachi Ltd., Tokyo, Japan) at 490 nm using the known concentrations of D-glucose as standards.

Enzyme assay

A litter sub-sample was finely chopped (2 mm×2 mm squares) and used to make a slurry (using a blender for 1 min) with 75 mL of 50 mM acetate buffer (pH 5). For all sampling date, 2 g fresh litter was used for the enzyme assay. The activities of four C-related enzymes: phenoloxidase (E.C. 1.10.3.2 and E.C. 1.14.18.1), peroxidase (E.C. 1.11.1.7), β-glucosidase (E.C. 3.2.1.21) and endocellulase (E.C. 3.2.1.4) were monitored. The phenoloxidase and peroxidase activities were measured using L-3,4-dihydroxy-phenyl-alanine (L-DOPA) (Sinsabaugh *et al*. 2002; Kourtev *et al*. 2002). The substrate (10 mM) was dissolved in 50 mM acetate buffer (pH 5). The oxidase samples also contained hydrogen peroxide (H_2O_2). The peroxidase activity was derived by subtracting phenol oxidase activity from the total oxidase activity. The litter slurry (2 mL) was incubated with 2 mL of the substrate (and 0.2 ml of 0.03% H_2O_2 for total oxidase) at 20°C for 1 h. Parallel substrate and sample controls were also included. The samples were then centrifuged and the supernatant was directly used to measure its absorbance at 460 nm.

β-Glucosidase activity was measured using the *p*-nitrophenol (*p*NP) method (Kourtev *et al*. 2002; Sinsabaugh *et al*. 1993). The 10 mM substrate *p*NP-β-D-glucopyranoside was dissolved in 50 mM acetate buffer (pH 5). Two milliliter litter slurry was incubated with 2 mL of the substrate at 20°C for 2 h. The 2-mL aliquots from the litter slurries were removed from the solution under constant stirring. Parallel substrate and sample controls were also included. After incubation, the test tubes containing

the samples were centrifuged at 2000 rpm for 5 min and 1-mL supernatant was transferred to a tube containing 0.2 mL of 1 N sodium hydroxide (NaOH). The solutions were then brought up to 10 mL and the absorbance was measured at 410 nm. Enzyme activities were expressed as μM substrate $\cdot g^{-1} \cdot h^{-1}$.

Endocellulase activity was measured viscometrically using carboxymethylcellulose (CMC) (Almin and Eriksson 1967). This method determines the rate of viscosity decrease, which results from polymer degradation by the enzyme action. One millilitre litter slurry was incubated with 2 mL of 1.25% CMC for 2 h at 20°C. Afterwards, the samples were centrifuged and the supernatant viscosity was measured as the fall velocity in a small-bore pipette. The activity (proportional to absolute activity) was expressed in units $g^{-1} \cdot h^{-1}$.

Data analysis

The model for constant potential mass loss (Olson 1963) is represented by the following equation:

$$X/X_0 = e^{-kt} \quad (1)$$

where, X/X_0 is the remaining mass at time t, X the mass remaining at time t, X_0 the original mass, k the decomposition coefficient, and t the time. The exponential model was fit to the data using least squares regression of the natural logarithm of mean fraction mass remaining (Kuperman 1999).

The data were expressed as mean ± SE. Differences between the two temperatures and the two sites were tested using *t*-test. Data were checked for deviations from normality and homogeneity of variance prior to analysis. Measurements on each sample were made in triplicate. Pearson correlation coefficients were calculated between cumulative mass loss and cumulative enzyme activities. Statistical significance for all tests was set at $p<0.05$. The above analyses were obtained by the SPSS statistical software package version 11.0 (SPSS Inc, Chicago, Illinois 60606, USA).

Results

Mass loss

Fig. 1 A and B demonstrated the decomposition patterns of leaf litter for each temperature treatment. With each treatment, the mass loss of leaf litter increased exponentially with increasing time and was characterized by an initial fast rate of disappearance followed by a subsequent slow rate. The regression equations simulating decomposition rates over time were quite well for each treatment ($r^2>0.8$, Table 1). There was no difference in mass loss of leaf litter between two microbial decomposer communities derived from broadleaf forest (DBF) and coniferous forest (DCF) at 20°C at the initial 30 days incubation. Conversely, the mass loss of leaf litter driven by DBF was higher than that of DCF at 30°C at the first sampling period. In later sampling times, the litter mass loss driven by DBF was higher than that of the DCF at 20°C, and the cumulative mass loss in the end of incubation was 44.9% for DBF and 38.1% for DCF (Fig. 1 A and B). However, at 30°C the difference in mass loss between the two forest types was not significant at later sampling periods. Additionally, at 20°C the decomposition coefficient for DBF (0.144) was also higher than that of DCF (0.111) (Table 1). A temperature increase did not result in a significant difference in litter mass loss for DCF, but significantly ($P<0.05$) reduced the litter mass loss for DBF by approximately 6% at the last sampling time.

Table 1. Leaf litter decomposition coefficient (k) for the decomposer communities from coniferous forest and broadleaf forest at 20°C and 30°C.

Forest type	20°C		30°C	
	k	r^2	k	r^2
Coniferous forest	0.111	0.807	0.111	0.805
Broadleaf forest	0.144	0.858	0.108	0.803

Prior to treatment, the initial average lignin concentration of *C. eyrei* leaf litter was 31.2% of dry mass. Difference in lignin loss were not significant between microbial decomposers from two forest types at 20°C in the first sampling time, but lignin loss of microbial decomposers in DBF was higher than that in DCF in later samplings, exceeding 6.0% lignin loss at the last sampling time (Fig. 1 C and D; Table 2). The differences in lignin loss between the two forest stands were similar to that in the mass loss of leaf litter at 30°C; which the DBF lignin loss at initial 30 days was higher than that in DCF, but their differences were not significant in later days. At the end of incubation, the higher temperature significantly ($P<0.05$) increased the lignin decomposition for both DCF by 9.8% and DBF by 11.1% (Table 2).

Table 2. The difference in mass loss of litter, lignin and total carbohydrate after 120 day's incubation at different temperatures

Forest type	20°C		
	Mass loss	Lignin loss	Total carbohydrate loss
Coniferous forest	38.1±0.4Ba	22.3±2.1Bb	51.2±0.4Ba
Broadleaf forest	44.9±0.7Aa	28.8±1.5Ab	55.4±1.3Aa
Forest type	30°C		
	Mass loss	Lignin loss	Total Carbohydrate loss
Coniferous forest	38.1±0.9Aa	32.1±1.1Aa	50.7±0.3Ba
Broadleaf forest	38.9±3.5Ab	33.9±1.5Aa	53.1±1.3Ab

Note: Data in the same column followed by the different capital letter is significantly different and in the same row followed by the different small letter is significantly different according to t-test ($P<0.05$).

Also, prior to treatment the initial average concentration of total carbohydrate of *Castanopsis eyrei* leaf litter was 43.6%. Total carbohydrate loss was much higher than the lignin loss, exceeding a 50% carbohydrate loss, (Fig. 1 E and F; Table 2). Carbohydrate loss in DBF was marginally higher than that in DCF at both 20°C (4.2% excess) and 30°C (2.4% excess) (Table 2). Carbohydrate loss in DBF at 20°C was statistically significantly ($P<0.05$) higher by 2.3% than that at 30 °C; but the difference was not found in DCF (Table 2).

Enzyme activities

Fig. 2 showed that DBF and DCF had a similar changing pattern for enzyme activities over time during incubation at both 20°C and 30°C. Phenoloxidase activity incubated at 20°C showed an increasing trend, and the maximum occurred at the 60th day. However, maximum phenoloxidase activity at 30°C occurred at the 30th day and then decreased gradually (Fig. 2 A and B).

Phenoloxidase activity in DBF was significantly (P<0.05) lower than that in DCF at both 20°C and 30°C. Analyses indicated that an increase in temperature did not result in significant difference in phenoloxidase activity between DCF and DBF.

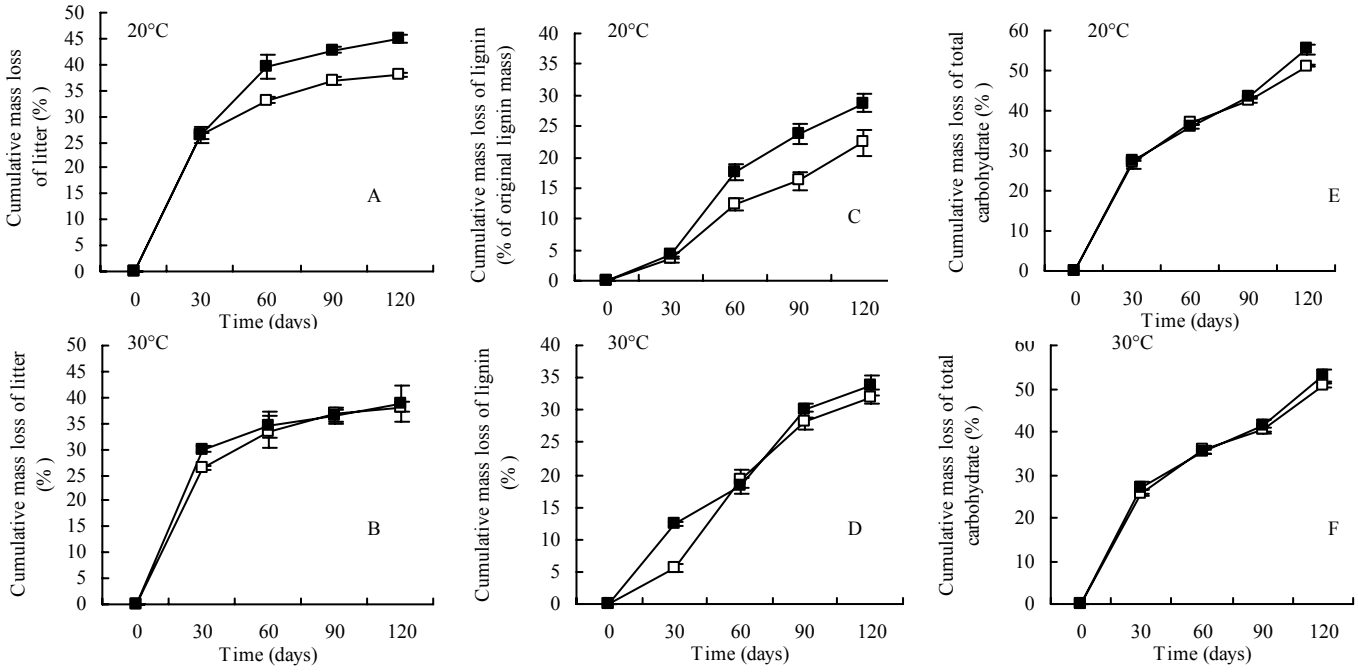

Fig. 1 The cumulative mass loss of litter, lignin, and carbohydrate of *Castanopsis eyrei* during 120 days' incubation at 20°C and at 30°C driven by microbial decomposers from coniferous forest (open squares) and evergreen broadleaf forest (black squares).

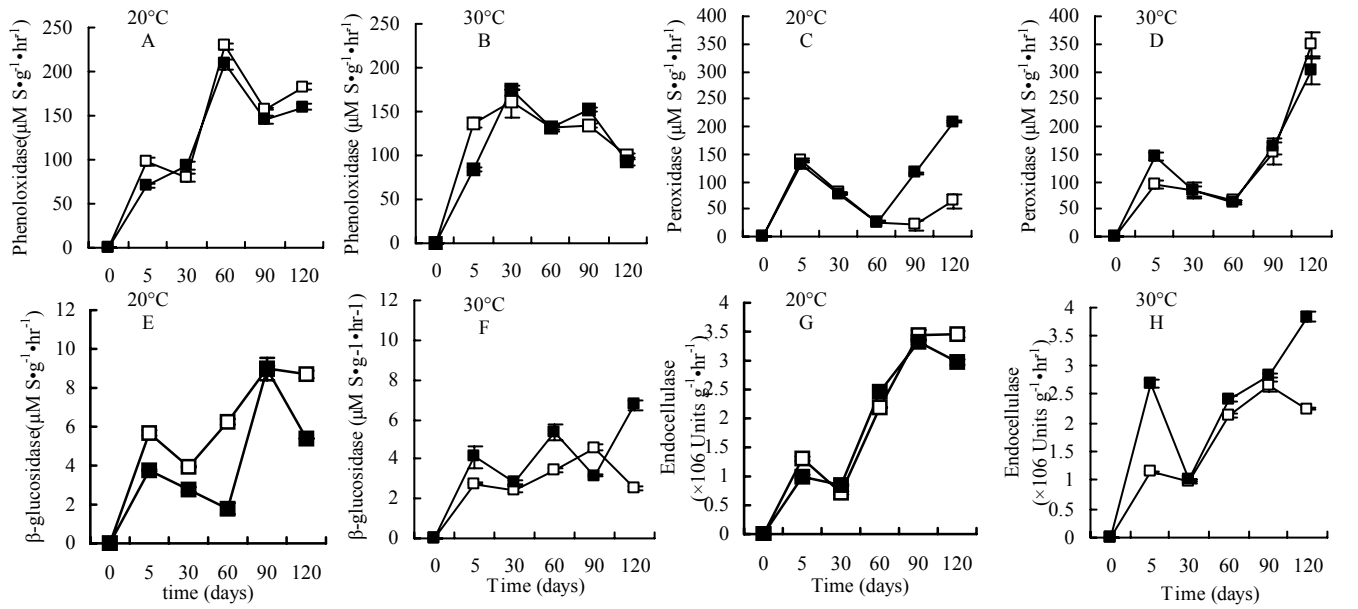

Fig. 2 Phenoloxidase, peroxidase, β-glucosidase and endocellulase activities during decomposition of *Castanopsis eyrei* over time at 20°C and 30°C driven by microbial decomposers from coniferous forest (open squares) and evergreen broadleaf forest (black squares)

Prior to the 60-day sampling period the peroxidase activity in DCF and DBF exhibited a gradually decreasing tendency at both temperatures, whereas the peroxidase activity began to increase steadily after 60 days (Fig. 2 C and D). At temperature of 20°C, DCF and DBF showed the identical peroxidase activity until the 60th day incubation, while in turn the enzyme activity in DBF was significantly (P<0.001) higher than that in DCF after that incubated duration. At 30°C, difference in peroxidase between DCF and DBF was not significant throughout incubation. The temperature rising significantly (P<0.001) improved the peroxidase activity for two forest stands.

By contrast with other enzymes, at both temperatures β-glucosidase showed a more variable pattern over time, but also an increasing activity over time (Fig. 2 E and F). Comparing β-glucosidase activity between the two temperatures, DBF and DCF showed opposite trends, for instance, β-glucosidase activity

in DBF at 20°C was significantly (P<0.001) lower than that in DCF, oppositely the activity was significantly (P<0.001) higher than DCF at 30°C. β-Glucosidase activity in DCF was significantly lower at 30°C than at 20°C, while no difference in the activity occurred in DBF.

Table 3. Correlation coefficients (r) for the relationship between mass loss and enzyme activity during 120 days' incubation

Variables	20°C		30°C	
	Coniferous forest	Broadleaf forest	Coniferous forest	Broadleaf forest
MLLT-GLU	0.930*	0.813NS	0.960*	0.973*
MLLT-END	0.921*	0.893*	0.945*	0.956*
MLLT-PHE	0.969*	0.942*	0.965*	0.975*
MLLT-PER	0.854NS	0.739	0.801	0.887*
MLCH-GLU	0.985**	0.971*	0.951*	0.967*
MLCH-END	0.981**	0.994**	0.973*	0.981**
MLLG-PHE	0.997**	0.986**	0.981**	0.993**
MLLG-PER	0.947*	0.842*	0.835*	0.919*

Note: MLLT, mass loss of litter; MLLG, mass loss of lignin; MLCH, mass loss of total carbohydrate; GLU, β-glucosidase; END, endocellulase; PHE, phenoloxidase; PER, peroxidase. ** P<0.01, * P<0.05, NS not significant.

Similarly to the above mentioned enzymes, the general of endocellulase activity over time also showed an increase trend both at 20°C and 30°C (Fig. 2 G and H). But like β-glucosidase at 20°C DBF had significantly lower endocellulase activity than DCF, oppositely at 30°C, DBF had significantly higher endocellulase activity compared to DCF. The temperature increase significantly (P<0.001) reduced the endocellulase activity for DCF, while it significantly (P<0.001) raised endocellulase activity for DBF.

Discussion

Previous studies have suggested that litter decomposition of mature evergreen broadleaf forest stands is faster than that of pine forest stands (Mo *et al*. 2006). The present study suggested that it was true at a standard temperature of 20°C, but at the higher temperature of 30°C there was no difference in decomposition rates of leaf litter between the two forest types. The diversity in plant species might be responsible for these results. Some researchers (Pennanen *et al*. 1999; De Santo *et al*. 2002; Thormann *et al*. 2003; Gartner and Cardon 2004) have suggested that litter species diversity on the ground could affect colonization and succession of microorganism and also directly affect the abundance, composition, and activity of the decomposer community. Broadleaf forest generally showed higher diversity in plant species than coniferous forest singly dominated by *Pinus massoniana*. Thus, broadleaf forest probably had higher diversity of microbial decomposers. It means a higher diversity of functional groups of microbial decomposers, leading to greater mass loss of leaf litter at the standard temperature. In contrast, at higher temperature of 30°C, the difference in leaf litter decomposition was not significant between the two forest types. Maybe the functional groups of microbial decomposers mentioned above, were sensitive to higher temperature, thus the microorganisms growths were inhibit at higher temperature. Broadleaf forest had higher lignin loss than coniferous forest at 20°C but the difference was not found at 30°C, which partly accounted for the difference in litter mass loss between broadleaf forest and coniferous forest. On the enzyme level, β-glucosidase, endocellulase and phenoloxidase had strong correlation with litter mass loss in most cases (Table 3), but the contribution of each enzyme mentioned above to mass loss of leaf litter varied between DBF and DCF. The reason was that the response of these enzyme activities and mass loss of leaf litter to forest type (coniferous and broadleaf forests) was not equal in most cases, and neither of enzymes above could be primarily responsible for the mass loss of leaf litter. Although the response of peroxidase to forest type was consistent with that response of mass loss leaf litter, this enzyme had a poor relationship with litter mass loss in most cases. Therefore, peroxidase probably contributed less to mass loss of leaf litter.

Response of litter decomposition to temperature at the community scale can greatly influence the balance of C storage. Some researches reported that higher temperature accelerated the decomposition of organic carbon (Hobbie 1996; Scowcroft *et al*. 2000). Vitousek *et al*. (1994) also reported that the litter decomposition rate increased four to eleven-fold for a 10°C increase in temperature. However, our results showed that the increase in temperature did not result in a change in mass loss of *Castanopsis eyrei* leaf litter driven by DCF, whereas the litter mass loss driven by DBF decreased with temperature increase. Giardina and Ryan (2000) also reported that increased temperature alone would not stimulate the decomposition of organic carbon in soil. Temperature increase probably inhibited the growth of some functional groups of decomposer in broadleaf forest. Since temperature increase improved lignin decomposition, decomposer in broadleaf forest responding to temperature increase did not result from ligninolytic fungi. These decomposers in broadleaf forest growing on the cool ground were possibly sensitive to higher temperature, whereas the microbial decomposers of coniferous forest living in warm and sun-shining habitat probably had a high adaptability to higher temperature. This indicated that the fungi from coniferous forest had the ability of regulating decomposition. On the enzyme scale, to DCF, the increasing temperature inhibited the activity of β-glucosidase, endocellulase and phenoloxidase, except for increasing peroxidase activity. The response of these enzymes to temperature increase probably partly counteracted each other, thus the decomposition rate for coniferous forest treatment did not show sensitivity to temperature increase. To DBF, the increasing temperature did not inhibit any enzyme in our experiment, but reduced the mass loss of leaf litter. Therefore, the four enzymes were not primarily responsible for mass loss of leaf litter in DBF. Some functional groups of microbial decomposer were sensitive to temperature change, but some exception had strong resistance to increasing temperature. This was probably determined by the composition and structure of decomposer community.

It was expected that DBF had higher lignin decomposition rate than DCF at temperature of 20°C. Some ligninolytic fungus, especially basidiomycetes, often was found more frequently in older forest types rather than in younger ones (Stokland and Kauserud 2004). Mature broadleaf forest presumably had more ligninolytic fungi that were responsible for the higher lignin decomposition at the lower temperature. Higher peroxidase activity in DBF at lower temperature also partly contributed to the difference between two forest stands. However, there was no difference in lignin decomposition between two forest types at temperature of 30°C, which was consistent with the response of

peroxidase to forest type. Higher temperature probably greatly stimulated the secretion of ligninolytic enzyme, despite coniferous forest possibly had less ligninolytic fungi than broadleaf forest. But improved enzyme activities would equalize the insufficiency in the quantity of ligninolytic fungi for DCF. The fact that higher temperature improved the peroxidase activity also further validated the speculation above. The strong relationship between lignin loss and peroxidase (Table 3) showed that peroxidase was probably responsible for the lignin loss at higher temperature. Probably peroxidase was the most important ligninolytic enzyme excreted by microorganism from the coniferous and broadleaf forest. Increased temperature appeared to result in great lignin degradation in organic matter (Huang *et al*. 1998). Tuomela *et al*. (2000) also found in compost experiment that the elevated temperatures were essential for rapid lignin degradation and the optimum temperature for thermophilic fungi and lignin degradation was 40−50°C. Our results also indicated that a 10°C increase in temperature accelerated the lignin decomposition for two forest stands. However, Osono and Takeda (2006) reported that a 10°C increase in temperature did not influence lignin mass loss below 20°C. Ligninolytic decomposition fungi had strong sensitivity to the temperature increase only at temperature beyond 20°C. Also, lignin loss at higher temperature probably resulted from the fact that the higher temperature improved the peroxidase activity. Phenoloxidase was not sensitive to temperature increase, thus it did not contribute to the difference in lignin loss between the two temperatures.

DBF resulted in higher carbohydrate decomposition compared to DCF at temperature of 20°C and 30°C. This suggested that some functional groups of cellulolytic decomposers existed in the broadleaf forest and were not sensitive to temperature increase. However, DBF had lower activity of β-glucosidase and endocellulase by contrast to DCF at 20°C. This indicated that other enzymes excepting β-glucosidase and endocellulase were responsible for the carbohydrate loss at the lower temperature. But DBF had higher enzyme activity than DCF at 30°C. The possible reason was that higher temperature improved some enzyme activity hydrolyzing carbohydrate in DBF. The fact that higher temperature increased endocellulose activity in DBF also further validated the speculation above. Generally, increased temperature resulted in the rapid carbohydrates depletion (Anderson and Hetherington 1999). Osono and Takeda (2006) also reported that mass loss of carbohydrates was higher at 20°C than at 10°C. However, in our experiment, the elevated temperature reduced the carbohydrate decomposition. Perhaps different substrate materials influenced the response of carbohydrate decomposition to temperature (LuxhØi *et al*. 2002; Hao *et al*. 2006). Another possible explanation is that in the context of high temperature the increase in temperature presumably reduced the activity of cellulolytic fungi. The higher temperature significantly inhibited cellulolytic enzyme activity in DCF, and there was strong correlation between endocellulase activity and carbohydrate loss. All these indicated that endocellulase might be the dominant carbohydrate-hydrolyzing enzyme in DCF. But higher temperature improved endocellulase activity in DBF. Probably endocellulase was not the primary carbohydrate-hydrolyzing enzyme in DBF. The different response of carbohydrate decomposition and hydrolytic enzyme were presumably determined by the composition and structure of decomposer species of the two forest types.

Microorganism decomposer took some strategy in the mass loss of leaf litter to adapt the temperature increase. Temperature increase did not affect the mass loss of leaf litter for DCF. Although temperature increase improved the lignin loss, it also greatly reduced other organic chemical components for DCF. However, to DBF, temperature increase reduced the decomposition of leaf litter, which is primarily resulted from the carbohydrate reduction. The different response of DBF and DCF between leaf litter decomposition and loss of organic chemical components to temperature increase presumably resulted from the structure and composition of microorganism communities, especially ligninolytic and cellulolytic fungi decomposer. Although the strong correlation between enzyme activities and mass loss, in most cases the enzyme response to forest type and temperature was different from that response of mass loss. The reason was that more than one enzyme contributed to the mass loss of leaf litter and organic chemical components.

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